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Brood size manipulations in a spatially and temporally varying environment: male Tengmalm's owls pass increased reproductive costs to offspring

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Abstract: A key tool used to assess reproductive trade-offs in birds is brood size manipulation (BSM) experiments. Most BSM studies have examined the influence on short-term measures of reproductive output. Seldom evaluated are the effects on long-term fitness proxies under temporally or spatially varying environments. Unpredictable environments may affect reproductive trade-offs by altering the value of the brood or hampering optimization of reproductive effort. We reduced or enlarged broods of 140 male Tengmalm's owls *Aegolius funereus* by one chick during their first lifetime reproductive event. Males differed in age and bred in environments that varied in quality spatially (habitat structure) and temporally (abundance of main food). We measured the short-term (nestling number and condition) and long-term fitness proxies (survival, lifetime fledgling and recruits produced) until all experimental males disappeared from the population. BSMs did not affect fledgling number or condition, but in enlarged broods, offspring condition was lower in territories with a high proportion of agricultural fields. Importantly, no obvious impacts on long-term fitness proxies emerged; lifetime fledgling and recruit production of males did not differ between the BSM treatments. Thus, the primary caregiver (i.e. Tengmalm's owl males) passed increased reproductive costs to their offspring, which is in agreement with other studies investigating intergenerational reproductive trade-offs in species of intermediate lifespan. Reluctance to accept increased current reproductive costs in these systems highlights the potential for sexual conflict in bi-parental care systems in which one of the pair is the primary caregiver.

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1 Brood size manipulations in a spatially and temporally varying environment:
2 male Tengmalm's owls pass increased reproductive costs to offspring
3

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25 Author Contributions: EK conceived, designed and performed the experiments. RLT, MG, TL
26 analyzed the data. RLT, MG, TL, EK wrote the manuscript and provided editorial advice.

Summary

A key tool used to assess reproductive trade-offs in birds is brood size manipulation (BSM) experiments. Most BSM studies have examined the influence on short-term measures of reproductive output. Seldom evaluated are the effects on long-term fitness proxies under temporally or spatially varying environments. Unpredictable environments may affect reproductive trade-offs by altering the value of the brood or hampering optimization of reproductive effort. We reduced or enlarged broods of 140 male Tengmalm's owls *Aegolius funereus* by one chick during their first lifetime reproductive event. Males differed in age and bred in environments that varied in quality spatially (habitat structure) and temporally (abundance of main food). We measured the short-term (nestling number and condition) and long-term fitness proxies (survival, lifetime fledgling and recruits produced) until all experimental males disappeared from the population. BSMs did not affect fledgling number or condition, but in enlarged broods, offspring condition was lower in territories with a high proportion of agricultural fields. Importantly, no obvious impacts on long-term fitness proxies emerged; lifetime fledgling and recruit production of males did not differ between the BSM treatments. Thus, the primary caregiver (i.e. Tengmalm's owl males) passed increased reproductive costs to their offspring, which is in agreement with other studies investigating intergenerational reproductive trade-offs in species of intermediate lifespan. Reluctance to accept increased current reproductive costs in these systems highlights the potential for sexual conflict in bi-parental care systems in which one of the pair is the primary caregiver.

Key words: life-history trade-offs; clutch size; parental effort; residual reproductive value; quality vs. quantity of offspring

INTRODUCTION

Individual's trade-off available resources between survival and reproduction, this shapes a species' life history (Roff 1992). While some species prioritise reproduction in a particular reproductive season, others prioritise survival, and consequently, these species are longer-lived and only produce a few offspring per breeding attempt (Bennett and Owens 2002). Theory predicts that a large investment in one breeding attempt decreases future parent survival and reduces lifetime reproductive output, known as the "cost of reproduction hypothesis" (Williams 1966; Roff 1992). Moreover, within each reproductive attempt, individuals trade-off the quality and the quantity of the offspring produced (Santos and Nakawaga 2012), but the relative importance of this trade-off in determining fitness remains unclear.

Experiments are vital when investigating trade-offs, to avoid the effect of phenotypic correlations (Reznick et al. 2000). A key species group for experimental manipulation of reproductive effort have been altricial birds, in which clutch or brood size manipulations (BSMs) have been used to investigate the short-term costs of increased breeding effort to parents and their offspring (reviews in Roff 1992; Santos and Nakagawa 2012). However, most experiments have not assessed the long-term costs of BSMs and it remains unclear whether parents pass increased reproductive costs on to their offspring in terms of reduced "downstream" fitness (Santos and Nakagawa 2012). Of the studies that have examined long-term costs to parents with higher work-loads, none have detected an obvious impact on future reproductive success or survival (Roulin et al. 1999; Shutler et al. 2006; Erikstad et al. 2009). Offspring survival may nevertheless decrease in enlarged broods (de Koegel 1997). Thus, long-term fecundity measures are required to assess the real fitness consequences of BSMs to parents.

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77 Environmental conditions and individual phenotype may have a profound effect on
78 reproductive success. Nevertheless, such parameters are rarely assessed in BSMs.
79 Unpredictable environments can hamper individual optimization of current reproductive
80 effort (Morris 1987; Pettifor et al. 1988; Korpimäki and Rita 1996), or by altering the
81 perceived value of the brood following initial reproductive investment decisions (Lessells
82 1993). Individual traits such as age-specific reproductive costs (Descamps et al. 2009a), or
83 age-specific reproductive investment may further affect reproductive output (Cotter et al.
84 2011). Consequently, to understand how individuals optimize their reproductive effort, long-
85 term studies that use reliable fitness proxies and include variation in environmental conditions
86 are needed (Roff and Fairbairn 2007).

87

88 Here we experimentally altered brood size of the first lifetime breeding attempt of male
89 Tengmalm's owls (*Aegolius funereus*) and determined their subsequent lifetime reproductive
90 success (LRS). Males of this species have an average lifespan of 3.5 years (1 – 11 years;
91 Korpimäki and Hakkarainen 2012). In owls and diurnal raptors, the male provides nearly all
92 food for the female during egg laying, incubation and brooding, as well as for the fledglings
93 until their independence (Korpimäki 1992; Eldegard and Sonerud 2009). Because
94 Tengmalm's owl males are faithful to their breeding territory after their first breeding attempt
95 (Korpimäki 1993), we were able to estimate the lifetime reproductive success of experimental
96 males. As measures of LRS we used lifetime fledglings produced (LFP) and lifetime recruits
97 produced (LRP); both are good proxies for the long-term genetic contribution of an individual
98 to a population (Brommer et al. 2004).

99

To account for variation in environmental quality, we measured both spatial and temporal variation in territory quality. Tengmalm's owl males breeding in territories with a high proportion of old-growth forests have a higher survival and LRS than males breeding in territories dominated by agricultural fields (Laaksonen et al. 2004; Hakkarainen et al. 2008). Moreover, the abundance of Tengmalm's owl main prey, *Microtus* and *Myodes* voles that fluctuate in approximate 3-year cycles, affects breeding success and survival. In years of increasing vole abundance, owls have higher breeding success than in years of decreasing or low vole abundance (Korpimäki 1992; Laaksonen et al. 2002). We used this spatial and temporal variation to assess specifically how these may interact with BSMs to affect parental care investment trade-offs.

We tested the following four hypotheses: (i) Males that provision enlarged broods and increased their parental effort may show decreased future reproductive potential, shown as reduced lifetime breeding attempts or reduced success in lifetime fledgling or recruit production. (ii) Alternatively, males may pass on the cost of raising enlarged broods to their offspring, lowering the offspring phenotypic quality (i.e. reduced body size, increased mortality) compared to offspring of reduced or control broods, with no effect on lifetime reproductive output. (iii) The mismatch that BSMs create depends on environmental conditions in that breeding season and territory, where raising an enlarged brood under poor conditions may create additional costs to the parent or the offspring. (iv) We predict that male age would alter male investment where older males increase their reproductive investment more than younger males.

METHODS

We studied Tengmalm's owls in a 1300 km² area in western Finland (63° N, 23° E). Since 1973, all nest-boxes (N = 420 during 1983-1987; N = 470 from 1988 onwards) and known natural cavities (N ~ 30) were repeatedly inspected each spring (details on field methods given in e.g. Korpimäki 1992, Korpimäki and Hakkarainen 2012). We collected breeding data from all nests and caught parents whenever possible.

We conducted BSMs on a subset of Tengmalm's owl nests during four breeding seasons. Two seasons (1985, 1988) were characterised by increasing, and two years (1986, 1989) by decreasing, vole abundances (Table 1). An earlier study that used data from 1985 and 1986 investigated the short-term costs of BSMs (Korpimäki 1988), finding no short-term fitness cost or benefit of raising an enlarged brood. Here, we focus on the long-term fitness consequences of BSMs using a much larger sample.

To conduct brood manipulations, we selected nest pairs with similar laying dates and clutch sizes. From a randomly selected nest, we transferred one recently hatched nestling (between 2 and 6 days old) to the other nest. A third nest with similar laying date and clutch size served as a control; this nest was visited but it remained un-manipulated. Brood manipulation thus produced nests with reduced (-1), enlarged (+1) and unchanged (0) broods. At the time of nestling transfer, we caught all female owls tending nests by hand. Nests were next visited when the nestlings were 10-18 days old, to trap males with a nest box trap, and again when they were 25-26 days old, to measure body mass and wing length, and to ring all chicks. We checked nests after the fledging of chicks, to determine the number of chicks that died before fledgling. Both males and females were ringed/re-trapped and aged to one-year-old or older based on moulting patterns (Hörnfeldt et al. 1988).

Up to 2001 and onwards, we have studied the population of Tengmalm's owl as per our normal protocols with breeding monitored at all nests in the study area (Korpimäki and Hakkarainen 2012). We focused male trapping effort on nests in the core study area where the majority of experimental males were breeding. Males are thought to be site faithful following first breeding (Korpimäki and Hakkarainen 2012). During this time, we trapped more than 75% of male owls (min. 50%, max. 95%) at their nests annually. This allowed us to follow the reproductive success of all experimental males to the end of their breeding career (lifespan up to 11 years; Korpimäki 1992; Korpimäki and Hakkarainen 2012). Uncaught males might have increased the error in the lifetime reproductive output data, but this error should be equal across treatment groups.

Long-term reproductive success was determined by counting the lifetime fledglings produced (LFP) and lifetime recruits produced (LRP) by experimental males. We also used nationwide ringing controls to provide data on recruits, offspring of experimental males that had settled outside the study area. Nationwide data were used to avoid substantial bias created by long-distance natal dispersal (Tinbergen 2005, Korpimäki and Hakkarainen 2012).

All males included in this study were in their first lifetime breeding attempt during the experimental year. We removed from the dataset any males that were manipulated twice. These mistakes were unavoidable because chick exchanges occurred during the early nestling phase when male identity at each nest was still unknown. Consequently sample sizes between reduced, enlarged and control broods differ (Table 1), and 1985 and 1986 sample sizes are reduced compared to those reported in Korpimäki (1988).

To assess habitat composition of the breeding territory, we used a 1000 m radius (314 ha) around the nest boxes as a proxy since it covers the approximate home range size of Tengmalm's Owls (ca. 200-500 ha; Santangeli et al. 2012). Land-use and forest resource data were obtained from Landsat TM 5 images, classified by the National Land Survey of Finland (Vuorela 1997). Only the proportion of old forests and proportion of agricultural fields were used, as these are the most relevant habitat variables identified for the reproductive success and LRS of Tengmalm's owls (Hakkarainen et al. 2003; Laaksonen et al. 2004). Habitat data were available for 117 of 140 territories, and were therefore analysed separately (see below).

Statistical analyses

We analysed data in three steps. Firstly, we ran generalised linear models (GLMs, using PROC GENMOD in SAS 9.1; SAS institute, Cary, North Carolina) to confirm pre-manipulation similarity in initial clutch size and initial number of nestlings. Then, using the same models, we tested to differences in the number of nestlings post-manipulation, the number of nestlings at ca. 14 days old (normal distribution, identity link), and the number of fledglings (all with Poisson distribution, log link) among BSM groups. The main fixed factors included were BSM treatment and vole cycle phase (class variables). Laying date (continuous variable), male age and female age (classes, first year or older) were included in initial models to test their impacts along with interactions between BSM and male age, BSM and vole cycle phase, BSM and laying date). Laying date is included in all models due to its influence on reproductive success in a season (Korpimäki and Hakkarainen 2012). In initial models, all variables of interest were included and non-significant terms (initially interactions and then main effects) were removed using backward elimination in order to produce a final model. BSM and vole cycle phase were always retained in final models due to the known importance

of vole cycle in determining breeding success (Laaksonen et al. 2002, 2004). Non-significant main effects were added one by one to final models to determine their effect. In no cases did non-significant main effects prove significant when added to the model.

For nestling condition, we used nestling as the sampling unit and modelled nestling mass using a linear mixed model (PROC MIXED, normal distribution, identity link). The same terms as above were included and nestling wing length (continuous variable) was included as a covariate to control for the effect of nestling size on nestling mass. Nest identity was included in this model as a random effect.

Secondly, we investigated how spatial (proportion of agricultural fields and old forests within a territory; continuous variable) and temporal (vole cycle) variation in territory quality interacted with the BSM in influencing nestling size and number in the year of the manipulation. To test this we ran GLMs (identity link, normal distribution) with vole cycle phase and the proportion of field and old forests in owl territories included along with their interactions with BSM to check for contrasting responses to spatial and temporal variables. Spatial data was available for 117 of 140 nests. We included the same dependent variables included in previous models.

Finally, we investigated the long-term effects of BSM, using the probability of a male breeding again (male survival), male lifetime fledgling production (LFP) and male lifetime recruit production (LRP) as fitness proxies. A generalized linear model with binomial distribution (logit link) was used to test the probability that a male Tengmalm's owl would breed in the future, and GLMs (with Poisson distribution, log link) to test for effects of BSM on LFP and LRP. These models included the main effects of BSM, and male age and vole

cycle phase during manipulation year. We tested LFP and LRP responses with and without the number of male lifetime breeding attempts, which is the major cause of LRS variation (Korpimäki 1992). A BSM effect on LFP or LRP arising from long-term costs should be apparent without this covariate; controlling for it allows focus on the influence of the manipulation year on LRS measures.

RESULTS

Effects of BSM in the experimental year

Neither clutch size nor initial number of nestlings differed between BSM treatments or males of varying age ($p > 0.15$, Fig. 1). Enlarged broods were larger than reduced broods after the manipulation (Table 2a, Fig. 1). The number of nestlings at ~14 days still differed significantly between the BSM groups (Table 2b, Fig. 1). There was also a significant BSM and vole cycle interaction explaining number of nestlings at 14 days (Table 2b, Fig. 1). During years of increasing vole abundance, enlarged broods remained larger than control or reduced broods. In years of decreasing vole abundance, enlarged broods lost chicks to mortality soon after the manipulations and broods did not differ in nestling number when we compared broods at 14 days of age (Fig. 2).

However, the number of fledglings did not differ between BSM groups (Table 2c, Fig. 1). Fledgling number was affected by male age, food abundance and fledgling condition influenced by habitat quality. The number of fledglings was higher in years of increasing vole abundance and for +1-year old males than in years of decreasing vole abundance and for yearling males (Table 2c). The body condition of fledglings was not influenced by BSM, but was influenced by laying date and vole cycle phase (Table 2d). Fledglings had lower body condition in poor vole years and later in the season. In addition, habitat quality influenced

fledgling quality, which decreased with an increasing proportion of agricultural field, but only in enlarged broods (slope estimate: $\beta \pm \text{SE} = -0.33 \pm 0.06$, $t = -5.72$, $P < 0.001$; Fig. 3; Table 2d). We detected no such effect in reduced or control broods (Fig. 3).

BSMs and the probability of future breeding

The probability of Tengmalm's owl males breeding after the experimental year (a proxy for male survival) was unaffected by BSMs ($df = 2$, $\chi^2 = 1.8$, $P = 0.41$) or food availability in the manipulation year ($df = 1$, $\chi^2 = 0.59$, $P = 0.44$), but was influenced by male age ($df = 1$, $\chi^2 = 4.39$, $P = 0.036$). Thus, males in different BSM groups did not differ in their final number of lifetime breeding attempts (Kruskal-Wallis $\chi^2 = 0.79$, $df = 2$, $P = 0.68$; mean lifetime breeding attempt $\pm \text{SE}$ for males rearing reduced broods: 1.40 ± 0.1 , control males: 1.46 ± 0.14 , males rearing an increased brood: 1.70 ± 0.21). Males breeding for the first time as a one-year-old in the year of the experiment averaged 1.61 ± 0.16 lifetime breeding attempts, while old males averaged 1.44 ± 0.09 lifetime breeding attempts, with no significant difference between age classes (Kruskal-Wallis $\chi^2 = 0.05$, $df = 1$, $P = 0.82$).

BSMs and lifetime reproductive success

BSMs appeared did not have an obvious effect on lifetime fledgling production (LFP) of males (back-transformed LS means estimates with asymmetrical 95% confidence limits, reduced brood: 5.03 (4.39 – 5.76); control: 5.40 (4.81 – 6.06), enlarged brood: 4.80 (4.17 – 5.52); see Table 3 for statistics). BSMs also had no clear effect on the number of lifetime recruits (LRP) either (back-transformed LS means estimates with asymmetrical 95% confidence limits, reduced brood: 0.17 (0.09 – 0.35), control: 0.27 (0.16 – 0.45), enlarged brood: 0.27 (0.16 – 0.48); Table 3). The number of lifetime breeding attempts influenced both LFP and LRP but results did not change when this term was removed from the models. The

vole cycle phase during the manipulation year significantly explained LFP and LRP: both these fitness proxies were larger for males breeding for the first time in an increasing phase of the vole cycle (LRP mean \pm SE = 0.49 ± 0.12 , $n = 49$) than for those first breeding in a decreasing phase (LRP mean \pm SE = 0.11 ± 0.04 , $n = 86$).

DISCUSSION

We examined the effects of a single brood size manipulation on reproductive trade-offs in both short and long-term fitness measures using a dataset of 140 Tengmalm's owl males. Most importantly, BSMs appeared not to have obvious effects on long-term fitness measures despite our single chick manipulation having the potential to change the LFP by about 18% (LFP mean = 5.35). This may stem from the fact that the final number of fledglings did not differ between treatment groups since brood reduction occurred in enlarged broods even under high food abundance. Nevertheless, a manipulation effect did persist for a part of the nestling period. In years with high food abundance, enlarged broods remained large during the first half of the nestling period, while in low food years increased broods soon suffered brood reduction. Therefore, between-year variation in vole abundance only had a short-term effect on BSMs, despite having a major effect on all phases of the Tengmalm's owl life cycle (Korpimäki and Hakkarainen 1991, 2012; Korpimäki 1992).

Our results suggest that Tengmalm's owl males did not alter their reproductive effort in response to BSMs to the extent required by the additional offspring, thus passing on the costs to their offspring. This ultimately led to increased brood loss in enlarged treatment broods, similar to the response of Eurasian kestrels *Falco tinnunculus* to BSMs in the same study area (Korpimäki and Rita 1996). This is consistent with the idea that longer-lived species favour self-maintenance over current reproductive investment, causing brood loss in enlarged broods

(Martin 1987; Bokony et al. 2009). The fact that under high food abundance brood size reduction of enlarged broods occurred later suggests that temporal variation in food abundance did affect brood manipulations to some extent. Indeed, Korpimäki (1988) suggested that the additional chicks were raised in good vole years; but our study with a larger sample size showed this did not happen. It appears that additional chicks survived longer due to the higher food availability in increase vole cycle and not due to the increased effort in male provisioning.

Our results suggest that Tengmalm's owl males are "optimizing" their brood sizes despite the unpredictable nature of temporally fluctuating food abundance. They do not seem to respond to an additional chick, either in good or poor environmental conditions, and thus seem to have fixed their effort at earlier stages of breeding. We would expect this if male effort or quality would already determine the clutch size. However, this is unlikely to be the case, as indicated by female age, not male age, affecting clutch size in Tengmalm's owls (Laaksonen et al. 2002). Clutch size appears to be determined by the female, rather than the male, phenotype. We nevertheless found that male age influenced the number and condition of nestlings, and fledglings. Older males produced more and better quality offspring independently of the BSM; however, they did not increase their investment when rearing an enlarged brood. This suggests that older males are generally better providers than young males, but that both of them are working at a fixed level. Females instead might be responsive to the current conditions; they for example decreased provisioning effort during the late nestling period when provided supplemental food (whereas the males did not) (Eldegard and Sonerud 2010; see also Eldegard and Sonerud 2012). Unfortunately, our data does not allow us to examine the influence of female behaviour at the late nestling stages when they also provision the

brood, as this might have revealed if females compensated according to the need or reduced their effort in response to the brood size manipulations.

Habitat quality affects the breeding success and survival of Tengmalm's owls (Hakkarainen et al. 2003; Laaksonen et al. 2004), and thus could alter the offspring quantity-quality trade-off. We found that habitat quality affected the outcome of BSMs in the short-term. In enlarged broods, chicks showed decreasing body condition as the proportion of field in a territory increased. Similarly, blue tits (*Cyanistes caeruleus*) were unable to raise enlarged broods in low quality habitat (Tremblay et al. 2003). However, empirical evidence of the costs of reproduction under varying environmental quality is rare. Our study found no long-term fitness effects of BSMs interacting with habitat quality, but long-lived common eiders (*Somateria mollissima*), reproducing under unfavourable conditions had lower breeder survival (Descamps et al. 2009b). Indeed, suboptimal conditions in early life can reduce individual quality, resulting in lower recruitment probability (Griesser et al. 2006; Becker and Bradley 2007).

Experimental BSMs in Tengmalm's owls appeared not to influence male survival or long-term male fitness (LFP, LRP). A quantitative summary of avian BSM studies (Santos and Nakagawa 2012) found that females generally did not suffer any clear costs related to increased brood sizes, but males pay a survival cost from raising enlarged broods. They speculated that females, as the usual primary caregiver in most avian species, are unable to increase their feeding effort. Our results suggest that the primary caretaker of the brood (males in the case of Tengmalm's owls) might be unable to increase their reproductive effort significantly. Given that females do not contribute to feeding but rather also need to be fed, Tengmalm's owl males pass on increased costs of reproduction to the offspring. Moreover,

the short nights at northern latitudes constrain the hunting time available to strictly nocturnal Tengmalm's owl males (Zárybnická et al. 2012) and their sit-and-wait hunting strategy further limits their option to increase their reproductive investment.

Our manipulations mimicked the realistic decision to lay one more or less eggs (Lindén and Møller 1989). The experimental outcome was in accordance with life-history theory, which predicts that parents in longer-lived species do not elevate their reproductive effort in response to brood enlargements to the extent that it would affect their lifetime reproductive success. Our results suggest that individuals of the sex that are the primary caretaker of offspring do not alter their reproductive investment when facing an increased brood size. This indicates that they already are working close to their maximum provisioning capacity at natural levels of brood sizes. This pattern of parental investment has potentially important implications for understanding the evolution of bi-parental care, and for understanding how the conflicts between sexes over reproduction are resolved.

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470

Table 1. Number of males in the three BSM groups and the total used in analyses. The number of males in -1 (reduced) and +1 (enlarged) groups differ because only nests that were manipulated during the first breeding year of a male were included in analyses.

Vole cycle	Year	Treatment			Total
		-1	0	+1	
increasing vole abundance	1985	7	7	5	19
	1988	10	13	12	35
decreasing vole abundance	1986	8	10	8	26
	1989	18	24	18	60

Table 2. Results of generalised linear models that examine the effects of brood size manipulations (BSM) on a) number of chicks after the brood manipulation, b) number of chicks in the nest 14 days after hatching , c) number of fledglings , d) condition of fledglings (n = 116 nests with 531 nestlings). Factors placed in italics were not part of final model but we entered these singly to the final model to determine their effect. When habitat quality terms were entered into models, n = 119 (not applicable to the fledging condition model). We retained the brood size manipulation terms in all models. Only significant interactions are given.

Independent variable	d.f.	χ^2	P-value	Independent variable	d.f.	χ^2	P-value
a) Chicks after BSM ($R^2 = 0.28$) ^a				b) Chicks at ~14 days old ($R^2 = 0.23$) ^a			
BSM	2	48.80	<0.001	BSM	2	22.46	<0.001
Vole cycle phase	1	6.08	0.014	Vole cycle phase	1	5.25	0.02
% old forest	1	1.91	0.17	Male age	1	4.15	0.042
<i>Male age</i>	1	2.78	0.1	BSM*Vole cycle	2	9.82	0.007
<i>Laying date</i>	1	0.54	0.46	<i>Laying date</i>	1	1.49	0.22
<i>Female age</i>	1	2.48	0.12	<i>Female age</i>	1	2.23	0.14
<i>% field</i>	1	0.76	0.38	<i>% field</i>	1	0.19	0.66
				<i>% old forest</i>	1	0.74	0.39
c) Fledglings ($R^2 = 0.12$) ^a				d) Fledging condition ($R^2 = 0.62$) ^a			
BSM	2	1.11	0.58	BSM	2	0.10	0.91
Vole cycle phase	1	4.79	0.03	Vole cycle phase	1	12.32	0.001
Male age	1	3.97	0.05	Laying date	1	16.53	<0.001
<i>Laying date</i>	1	1.28	0.26	Wing length	1	130.36	<0.001

<i>Female age</i>	1	0.64	0.42	Male age	1	4.06	0.05
<i>% field</i>	1	1.14	0.71	<i>% field</i>	1	2.16	0.15
<i>% old forest</i>	1	0.31	0.58	BSM* <i>% field</i>	2	4.45	0.02
				<i>Female age</i>	1	1.98	0.1
				<i>% old forest</i>	1	1.63	0.21

484 ^aCalculated as $1 - (\sum(y_i - \hat{y}_i)^2 / \sum(y_i - \bar{Y})^2)$, where \bar{Y} represents the sample mean; \hat{y}_i predicted

485 value of the individual i ; y_i the observed value of individual i .

486

487 Table 3. Generalised linear models (log-link, Poisson distribution) on the lifetime production
 488 of fledglings (a) and recruits (b) in Tengmalm's owl males (n = 140) included in the BSM
 489 experiment. Factors placed in italics were not part of final model but we entered these singly
 490 to the final model to determine their effect.

Independent variable	d.f.	χ^2	P-value
a) Lifetime fledgling production ($R^2 = 0.51$) ^a			
BSM	2	1.82	0.40
Cycle	1	4.49	0.03
Lifetime breeding attempts	1	149.47	<0.001
<i>Male age</i>	<i>1</i>	<i>3.26</i>	<i>0.07</i>
b) Lifetime recruit production ($R^2 = 0.24$) ^a			
BSM	2	1.36	0.51
Cycle	1	13.30	<0.001
Lifetime breeding attempts	1	21.27	<0.001
<i>Male age</i>	<i>1</i>	<i>2.15</i>	<i>0.14</i>

491 ^a Calculated as $1 - (\sum(y_i - \hat{y}_i)^2 / \sum(y_i - \tilde{Y})^2)$, where \tilde{Y} represents the sample mean; \hat{y}_i predicted
 492 value of the individual i ; y_i the observed value of individual i .

493

494 Figure legends:

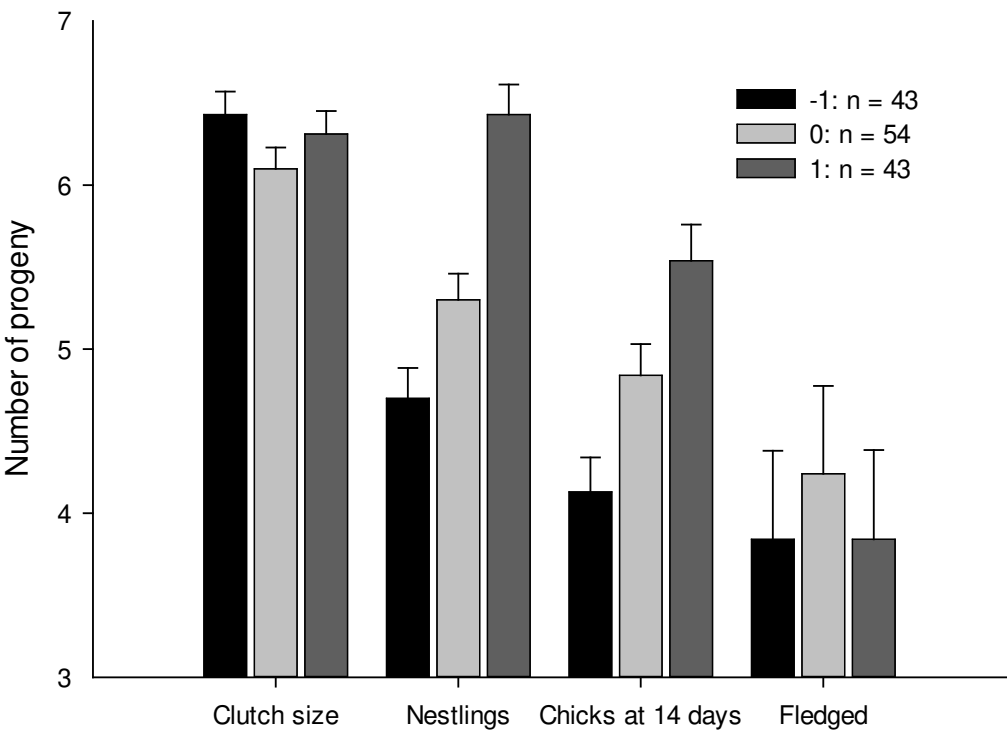
495 Fig. 1 Clutch size, number of nestlings after brood size manipulation, number of chicks at 14
496 days and number of fledglings in different treatment nests of Tengmalm's owl. Graph
497 presents LS mean estimate and standard errors, log back-transformed if needed. Post-hoc LS-
498 means comparisons indicated that all the treatment groups significantly differed from each
499 other in number of nestlings after manipulations (reduced vs. control: $p = 0.03$; reduced vs.
500 increased: $p < 0.001$; control vs. increased: $p < 0.001$) and in the number of 14 day old
501 nestlings (reduced vs. control: $p = 0.01$; reduced vs. increased: $p < 0.001$; control vs.
502 increased: $p = 0.02$).

503

504 Fig. 2 Number of 14 day old nestlings in increasing and decreasing prey abundance, in
505 reduced (-1), control (0) and enlarged (1) broods. Graph presents LS mean with standard
506 errors and number of nests in the three experimental groups are given on bars.

507

508 Fig. 3 Residual body mass from models of individual Tengmalm's owl fledglings against the
509 proportion (%) of agricultural field in the territory of reduced (A), control (B) and enlarged
510 (C) broods.



512

513

